THE BIOLOGY OF *DOA AMPLA* (GROTE) (LEPIDOPTERA: DOIDAE) ON ITS HOST PLANT *STILLINGIA TEXANA* (EUPHORBIACEAE)

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Abstract.—We confirm *Stillingia texana* L. (Euphorbiaceae) as a primary host plant of *Doa ampla* Grote (Lepidoptera: Doidae), document aspects of the biology, ecology, and behavior of larval and adult *D. ampla* on *S. texana*, and provide initial geographic distribution data for *D. ampla* in central Texas.

Key Words: gregarious behavior, aposematic coloration, group defense

Doa ampla (Grote) is one of five species in the genus *Doa* (Neumoegen and Dyar 1894). The familial placement of this group has a checkered history (Donahue and Brown 1987). The genus *Doa* has at times been placed in the Lymantriidae (Dyar 1903, Holland 1903, Barnes and McDunnough 1917, Bryk 1934), Hypsidae (Walton 1912), Pericopidae (Schaus 1927, McDunnough 1938, Peterson 1948), Dioptidae (Brues and Melander 1954), and Arctiidae (Franclemont 1983). The genera *Doa* and *Leuculodes* (which contains two species) currently are placed in the family Doidae within the superfamily Noctuoidea (Donahue and Brown 1987). According to Donahue and Brown, elevation of doid months to the family level represents an interim solution; however, Miller (1991) strongly supported family status.

All known host plants of *D. ampla* are in the family Euphorbiaceae. *Doa ampla* previously has been reared on *Euphorbia robusta* (Engelmann) in Colorado (Cockerell 1911), *E. incisa* Engelmann and *E. lurida* Engelmann in Arizona, and *Stillingia tex-* ana L. in Texas (Donahue and Brown 1987). *Doa ampla* occurs from Colorado east to Texas, southward to Durango and Nuevo León, Mexico, and west to Arizona (Donahue and Brown 1987). Aside from limited information on geographic distribution and host plant range, nothing is known of the biology and ecology of *D. ampla*. Here we confirm *S. texana* as a primary host plant of *D. ampla* in Texas, document aspects of the biology, ecology, and behavior of larval and adult stages, and provide distribution data for *D. ampla* in central Texas.

METHODS

Here we present the findings of field and laboratory studies conducted during the summers of 1996 and 1997. To confirm *S. texana* as a host plant of *D. ampla* (as evidenced by acceptance of *S. texana* for oviposition and the ability of *D. ampla* larvae to complete development successfully) we searched *S. texana* plants for ovipositing females, egg clusters, and larvae at three field sites. These field sites were located at Hon-

ey Creek State Natural Area (Comal Co., Texas), Pollard Refuge (Southwest Texas State University, Hays Co., Texas), and a privately owned site along Devils Backbone (Comal Co., Texas). We censused daily egg clusters located in the field to estimate timing events in the life cycle, describe larval behavior, and document natural enemies. In addition, we collected females from *S. texana* patches and introduced them onto potted *S. texana* plants in the laboratory to monitor oviposition. We subsequently monitored egg clusters daily to estimate rates of development for each instar at 21–23°C.

We gathered initial distribution and abundance data for *D. ampla* in south-central Texas by surveying *S. texana* populations in seven adjacent counties located along the eastern edge of the Edwards Plateau. Primary state roads were used to establish multiple transects across each county. All *S. texana* populations on each transect that were accessible through a public right-of-way were searched for *D. ampla* egg clusters and larvae. We recorded the location (latitude, longitude, and elevation) of sites containing *D. ampla* by use of a Magellan GPS unit to provide site records for this apparently uncommon species (see below). We recorded site characteristics of occupied and unoccupied plant populations to describe the habitat affinities of this herbivore.

Initial field observations indicated that groups of larvae are often capable of defoliating the host plant and thus must travel between host plants to complete development. To determine at which instar larvae are capable of dispersing to adjacent plants we field-tested the dispersal capabilities of first- through fourth-instar larvae. Five field-collected larvae of each instar were marked with fluorescent dye powder and placed on the ground in the center of a 1-m-diameter circular area bordered by a ring of *S. texana* plants. All trials were initiated in full sun between 1500 and 1600 to mimic the conditions under which late-instar larvae had been observed to move between plants. We then counted the number of lar-

vae that successfully traversed the 0.5-m distance to a *S. texana* stalk after nightfall, using a UV lamp, and again at 24 hours. In total, 20 larvae of each instar were tested.

To describe the pattern of movement of feeding groups within plants and the movement of individual larvae within the natal plant as feeding aggregations fragmented we marked all second-instar larvae in feeding aggregations on selected plants at the Honey Creek field site using fluorescent dye. For the duration of the second and third instar we then relocated these larvae daily during both day and night. Using *D. ampla* clutches located on a second set of focal plants, we then estimated the rate of dispersal (%) and dispersal distance of third-instar or older larvae from natal plants. On each focal plant we counted and marked all larvae present with a color of dye unique to that plant just prior to the onset of dispersal (i.e., immediately after the molt into the third instar). We then censused each focal plant and all other *S. texana* plants within 20 m of each focal plant for marked larvae daily during both day and night until larvae molted into the fifth instar. Relocated larvae were re-marked after each molt to maintain unique marks. We calculated percent dispersal as the ratio of the number of third-, fourth-, and fifth-instar larvae relocated on adjacent plants to the original number of third-instar larvae on each focal plant. The distribution of distances moved from natal plants was used to construct a dispersal profile for late-instar larvae. We then compared the distribution of larval dispersal distances to the distribution of near-neighbor interplant distances to gauge the ability of dispersing larvae to locate neighboring host plants. To determine if dispersal from the natal host plant is related to resource depletion, we recorded the percent of leaves remaining on each focal plant at the time that larvae began to disperse and then used regression techniques to test for the dependency of dispersal rate on resource availability per plant.

RESULTS AND DISCUSSION

Host plant confirmation.—At our field sites we observed female *D. ampla* in residence with newly deposited egg clusters on *S. texana,* and caged females readily oviposited on the leaves of *S. texana* in the lab. Following oviposition on *S. texana* in the laboratory, we subsequently reared 48 *D. ampla* larvae to pupae and reared 12 of those to adults. Voucher specimens are deposited in the Southwest Texas State University Entomology Collection. These observations confirm *S. texana* as a primary host of *D. ampla* in central Texas.

During our field studies we observed third- and fourth-instar *D. ampla* larvae rarely feeding on *Chamaesyce acuta* Engelmann (Euphorbiaceae). No egg masses were observed on *C. acuta,* however, and no larvae found on *C. acuta* were relocated the following day on the same plant. Thus, this feeding appears to occur only when late-instar larvae are in transit between *S. texana* plants (see below). In addition to *S. texana,* two other species of *Stillingia, S. sylvatica* I. M. Johnst. and *S. treculiana* (Muell. Arg.) I. M. Johnst., occur in Texas. The distribution of *S. sylvatica* overlaps the eastern and northern edges of the geographic range of *S. texana,* whereas *S. treculiana* overlaps along the southwestern edge of *S. texana*'s range. We were unable to locate either species within the seven counties we surveyed. Hence, whether these species serve as additional hosts for *D. ampla* in regions of overlap with *S. texana,* as bridges to other known euphorb host plants whose geographic distributions occur west of Texas, or as both, remains unknown.

Distribution of *D. ampla* in central Texas.—We collected *D. ampla* larvae feeding on *S. texana* in six of seven counties surveyed. Representative GPS latitude—longitude—elevation coordinates of collection sites within each county are Bandera (29°43.42N, 99°7.47W, 555 m); Comal (29°55.46N, 98°9.10W, 326 m); Gillespie (30°10.42N, 98°44.65W, 639 m); Hays (29°56.13N, 98°7.24W, 393 m); Real (29°42.67N, 99°43.82W, 543 m); and Uvalde (29°45.50N, 99°31.15W, 682 m) (Fig. 1). In addition, *D. ampla* has been collected in Blanco County, Texas, by R. Kendall (Pedernales Falls State Park; collection date, 1973; personal communication).

Habitat affinities.—The host plant, *S. texana,* is a common though patchily distributed perennial that ranges from Oklahoma to Coahuila, Mexico. In Texas, the species is restricted to the dry calcareous soils of the Edwards Plateau region of south-central Texas, west to Val Verde Co., and north to Wise and Collin counties (Fig. 1). Within south-central Texas, we found *S. texana* to occur in two markedly different ecological contexts: (1) dense contiguous patches covering up to several hectares in heavily grazed lowlands and (2) sparse, patchily distributed small populations typically located in Hill Country uplands associated with moderate to steep slopes (20–45°). In upland areas, *S. texana* is characteristically smaller and has fewer and shorter flowering stalks per root system (mean number stalks per plant [$\pm$ SE] upland = 4.2 $\pm$ 0.41, n = 30; lowland = 25.6 $\pm$ 1.9, n = 30; t = 11.4, P < 0.01; mean height tallest stalk per plant [$\pm$ SE] upland = 30.0 cm $\pm$ 1.4, n = 30; lowland = 37.6 $\pm$ 1.9, n = 30; t = 3.2, P < 0.01).

We searched extensively for *D. ampla* on *S. texana* in both lowland and upland settings. However, we never found *D. ampla* in lowland sites and only found it in a small percent of upland sites examined. Moreover, within upland habitats where *D. ampla* was present, we rarely encountered larvae. For example, at the Honey Creek site (a primary study site based on the availability of *D. ampla*) we found eggs or larvae on fewer than 1% of the 1,042 plants censused. Nighttime black light surveys conduced at each of our three field sites known to be occupied by *D. ampla* failed to attract adults during the oviposition period. Thus, *D. ampla* is relatively rare in our study region, appears to be a habitat spe-
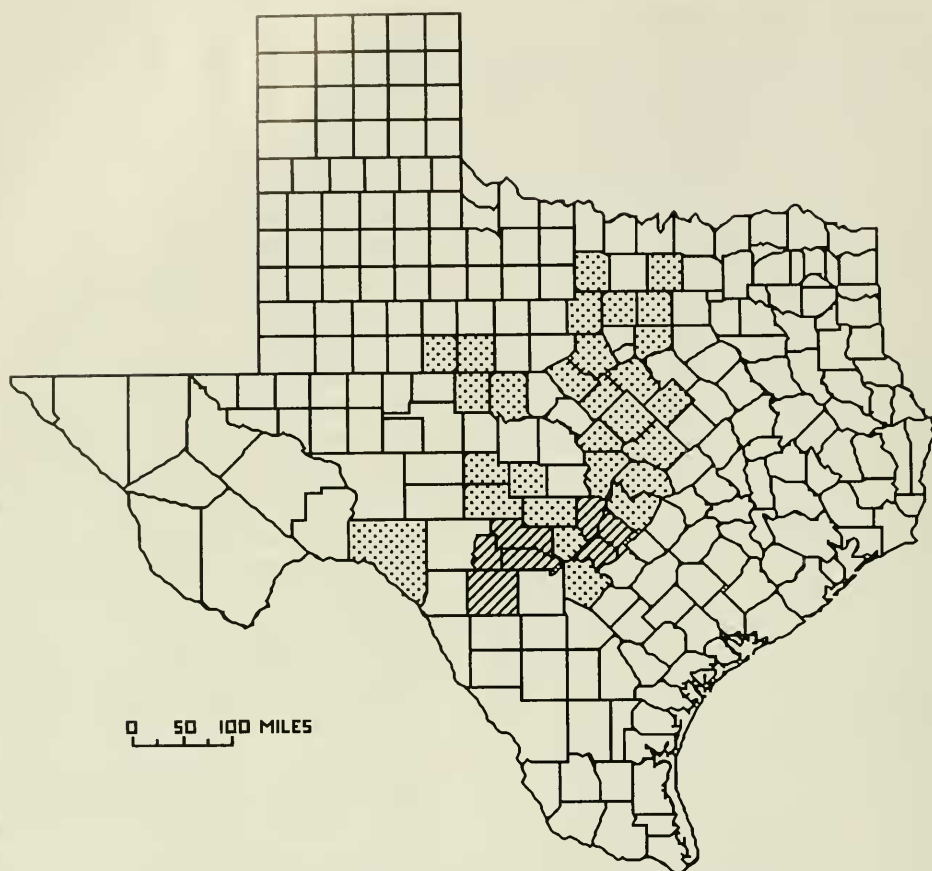
Fig. 1.   The known geographic distribution of *Stillingia texana* (light stippling) and *Doa ampla* (cross-hatched) in Texas.

cialist, and is rarely encountered even within its preferred habitat. Restriction of *D. ampla* to small, sparse upland plants is enigmatic in that the majority of larvae in all but very small groups must leave the natal host at some point during development and travel to a new host plant due to resource limitation (Braswell 1998). Therefore, the absence of *D. ampla* in lowland settings, where plants are larger (i.e., more resources per plant and therefore reduced need for between-plant travel) and more dense (i.e., reduced risk associated with interplant travel) is counterintuitive.

Life cycle.—*Doa ampla* is bivoltine in central Texas, exhibiting two narrowly overlapping generations per year. Oviposition occurs in early to mid-May and again

in mid-July. Eggs are laid in clusters of 7 to 231 eggs ($\bar{x} = 78.5 \pm 7.97$; $n = 44$) in parallel rows (Fig. 2). Egg clusters are placed on the underside of leaves on the upper one-fourth to one-third of the host plant. Occasionally, females covered a single leaf with eggs and moved to a second leaf to complete oviposition. Although field observations of females were rare and only a single female has been observed moving to a second leaf, the large discrepancy between the number of eggs on the first and second leaf suggests that the second group of eggs resulted from spillover of one clutch and not from a second female. Therefore, including spillover eggs, the mean number of eggs per clutch is 111.5 ± 11.51; $n = 31$. The larvae from different

egg clusters generally developed as independent groups. These egg cluster sizes are much larger than the 15 to 35 eggs per cluster reported for *D. ampla* on host plants in Arizona by Donahue and Brown (1987).

First- and second-instar *D. ampla* are gregarious (Fig. 3). As in *D. dora* Neumoegen and Dyar (Brown 1990) and *D. raspa* Druce (Dyar 1911), all instars of *D. ampla* are boldy colored and patterned, presumably an aposematic display associated with the toxicity of the host plant (Fig. 4). *Doa ampla* larvae complete five instars before pupation (Fig. 5). In the laboratory at 21–23°C, mean development time from egg hatch to pupation on cuttings of *S. texana* was 35.8 d (*n* = 48) and from pupation to adult emergence was 16.25 d (*n* = 12). In the field, mean larval development time (for the first generation) from first to fifth instar was 32.6 days; larvae spent 9.9 d (*n* = 8 groups) as first instars, 8.1 d (*n* = 13 groups) as second instars, 7.0 d (*n* = 9 groups) as third instars, and 7.6 d (*n* = 10 groups) as fourth instars. In both the laboratory and field, fifth-instar larvae leave the host plant to pupate. Pupation sites in the field are unknown. In the laboratory *D. ampla* fifth-instar larvae spun cocoons on the bottom, sides, or top of their nylon screen cages. In contrast, *D. dora* is know to pupate in the debris at the base of its host plant (Brown 1990). The cocoon of *D. ampla* described by Dyar (1912) is similar to that produced by *D. dora* (Brown 1990) and *D. raspa* (Dyar 1911). Individual larval groups followed in the field underwent ecdysis relatively synchronously (all larvae in each group completed ecdysis within 2 days). In early May, fifth-instar larvae appeared on new growth of the host plant prior to appearance of eggs, indicating that second-generation *D. ampla* overwinter as late instar larvae, pupae, or both.

Larval feeding behavior.—First- and second-instar larvae feed inside a communal nest loosely constructed of sparse silk threads (Fig. 3) and feed preferentially in the upper one-third of the host plant. These early-instar larvae feed by scraping the upper and lower surfaces of leaves leaving behind skeletonized leaf material. The leaves of *S. texana* are defended by a well-developed laticifer system that exudes latex when cut. Dussourd and Eisner (1987) demonstrated the defensive properties of latificer systems against herbivorous insects by showing that when drained of latex, formerly unpalatable leaves become palatable. Numerous insect feeding behaviors have been shown to represent adaptations designed to deactivate latificer-based host plant defenses (Dussourd and Denno 1991). Latex exudate is not visible when first- and second-instar *D. ampla* larvae feed on *S. texana*. Thus the mode of feeding of early-instar larvae may either allow them to avoid the laticifer system completely or scraping may result in small nicks that depressurize the laticifer system and diminish latex flow. If scraping depressurizes the system, individual larvae in groups may avoid ingesting large amounts of latex via the cumulative effect of the group on latex flow. We hypothesize that the behaviors of leaf scraping and gregarious feeding of early instars function as adaptations to diminish the functionality of or circumvent the host plant's laticifer system (Braswell 1998).

Beginning with the third instar, feeding aggregations dissolve and larval feeding behavior changes. Larvae continue to feed preferentially on the uppermost leaves of the host plant; however, third- through fifth-instar larvae bite through the entire leaf blade, often leaving behind only the main rib of the leaf. At this stage larvae are exposed directly to the latex exudate produced by the plant. On host plants with multiple stalks, larvae move to new stalks before feeding on the lower leaves of any stalk. Paradoxically, latex flow from injured leaves is highest in the uppermost portions of the host plant (Braswell 1998).

Larval dispersal capabilities.—When larval density is high, early-instar larvae quickly consume the preferred feeding area and, on small plants, begin to defoliate the

Fig. 2–3.   2, *Doa ampla* egg clusters on the underside of *Stillingia texana* leaves. 3, Second-instar *D. ampla* larvae exhibiting gregarious feeding behavior within a loose communal nest.

Fig. 4.   Fifth-instar *Doa ampla* larvae exhibiting the aposematic color pattern typical of all instars (bright yellow background color with longitudinal black bands).

entire plant. Because larvae typically avoid lower leaves of the plant, they must travel from the natal plant to another plant to continue feeding. We observed first- and second-instar larvae only on host plants with evidence of prior gregarious feeding (i.e., skeletonized leaves), suggesting that early instars do not disperse from the natal plant. Third- through fifth-instar larvae, however, were found on host plants lacking evidence of prior gregarious feeding, suggesting that these instars do disperse.

The results of our dispersal capability experiment confirmed these field observations. First- and second-instar larvae were incapable of traveling between host plants: none of 40 first- and second-instar larvae managed to move the 0.5-m linear distance required to reach a host plant, and all died within 24 h without traveling. However, 100% (40/40) of the third- and fourth-instar larvae tested traveled to a new host plant and initiated feeding within 8 h. Marking

and monitoring second-instar larvae in feeding aggregations showed that beginning with the third instar, concomitant with the switch in feeding mode, aggregations disintegrate and larvae independently move to new feeding positions on a plant, migrate to new host plants, or both.

An average of 82% of dye-marked third-instar larvae left their natal plants prior to completing development. Most larvae settled on near-neighbor plants, and no larvae traveled more than 5 m from the natal plant (Fig. 6). Mean dispersal distance of third-instar or older larvae (3.6 m $\pm$ 1.9, n = 126) did not differ from the mean distance between nearest-neighbor plants (1.6 m $\pm$ 7.6, n = 73) in the field population of *S. texana* we examined (t-test of means with unequal sample sizes and unequal variances, $P > 0.05$). These data suggest that whereas dispersing larvae may not always find the nearest-neighbor plant in relation to
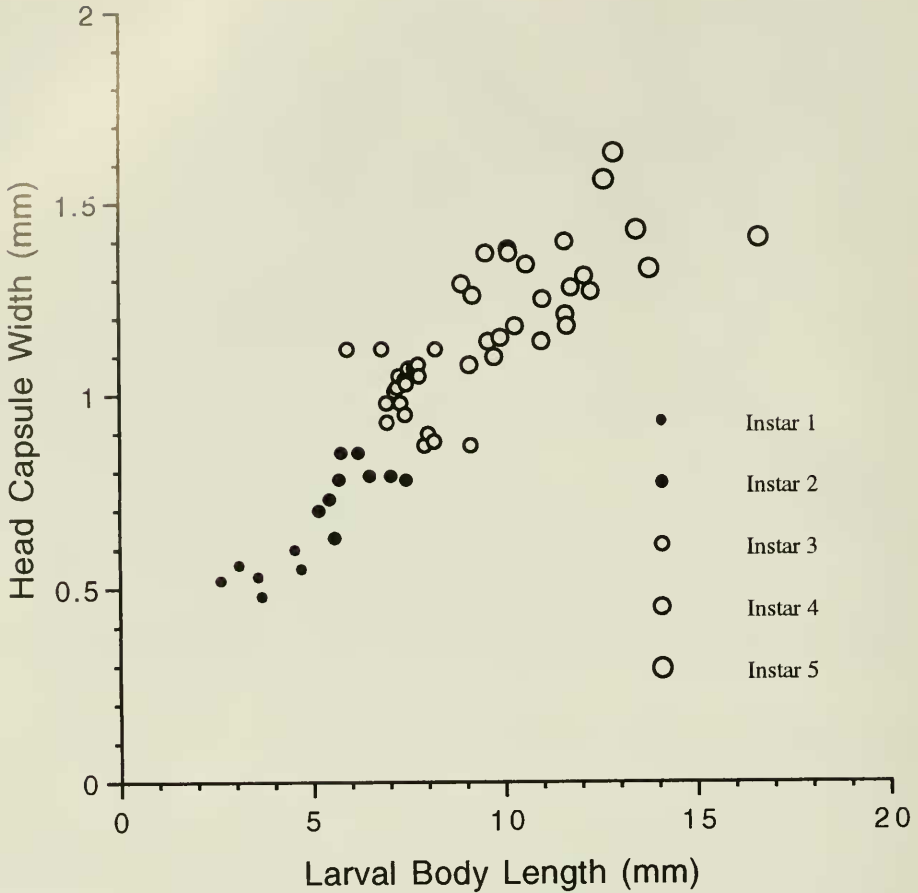
Fig. 5.   The relationship between head capsule width and body length for *Doa ampla* larvae, illustrating the five instars. Instars are represented by increasing-sized symbols. Instars exhibiting gregarious behavior are depicted with shaded symbols.

their natal plant, they are relatively adept at locating near-neighbor host plants.

Third-instar larvae can markedly reduce the number of leaves per plant prior to the onset of dispersal. The percent of leaves remaining per plant was inversely and non-linearly related to the number of third-instar larvae per group ($R^2 = 0.41$, $P < 0.05$; Fig. 7). Moreover, the percent of larvae that dispersed was negatively related to the percent of leaves remaining on the host plant ($R^2 = 0.38$, $P < 0.05$; Fig. 8). Therefore, dispersal rate appears to be influenced by resource availability as mediated by the interaction of larval group size and plant size.

Larval defensive behavior.—First and second instars when disturbed exhibit a head-flicking display. In this display, larvae rear up on the abdominal prolegs and thrash the head from side to side. The display occurs synchronously within the aggregation, and communication between larvae appears to be facilitated by the silk of the nest. Following continued disturbance, larvae drop from the host on silken threads. In later instars the head-flicking behavior decreases and larvae are more likely to drop to the ground when disturbed.

Predators and parasitoids.—Through two field seasons we observed relatively few
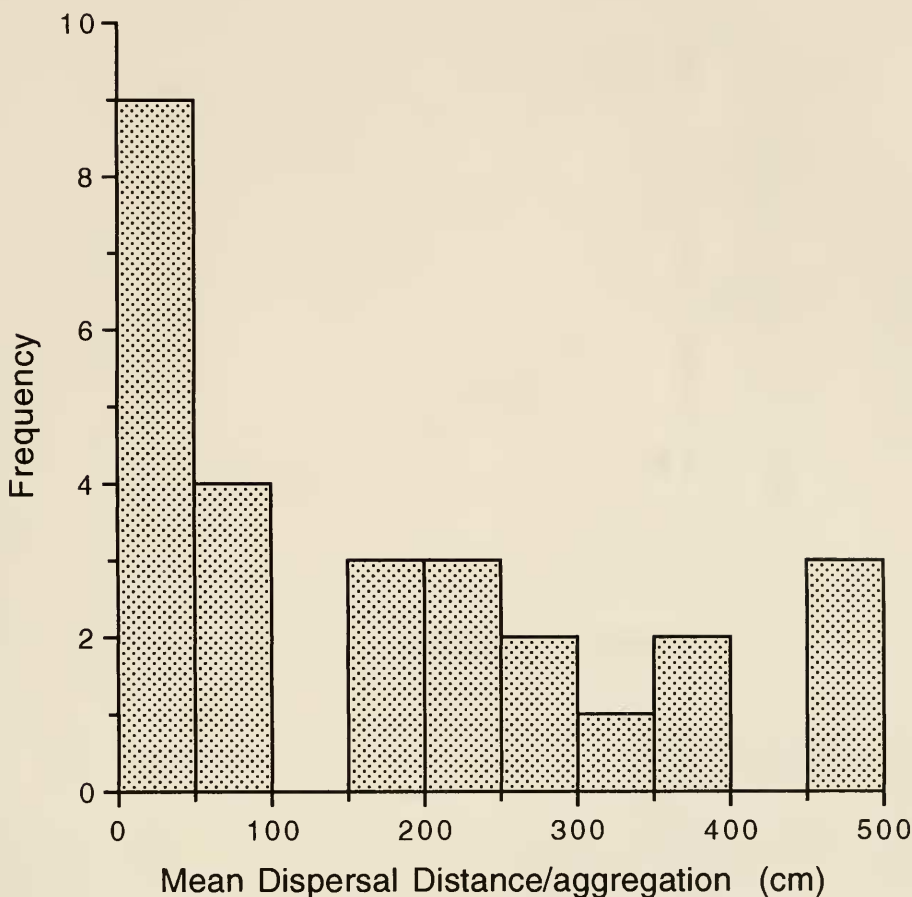
Fig. 6.   Mean dispersal distances/group for each of 25 groups of later-instar *D. ampla* larvae from their natal host plants under field conditions.

acts of larval predation and no acts of larval parasitism. No predation or parasitism of eggs was observed. The only successful acts of predation occurred on early-instar larvae by ants, which collectively attacked and removed single larvae. The only other act of predation we observed was an attack by a lynx spider (*Peucetia viricans* Hentz) on a third-instar larva. The spider bit and killed the larva but never returned to consume it. We collected later-instar larvae from both generations that appeared to have been parasitized as evidenced by their sluggish, unresponsive behavior. These animals did not feed and remained alive for months before dehydrating. No parasitoids emerged from these larvae.

SUMMARY

Stillingia texana is a host plant for *Doa ampla* in central Texas. Although this host plant is common throughout the eastern edge of the Edwards Plateau, often occurring in large, contiguously distributed populations, *D. ampla* is rarely encountered and is restricted to small, low-density patches of host plant occupying upland regions of moderate to steep slope. *Doa ampla* is bivoltine in central Texas and overwinters as late-instar larvae, pupae, or both. First- and second-instar larvae feed gregariously on leaf tissue by scraping the epidermal layer. This mode of feeding circumvents or reduces contact with the plant's la-
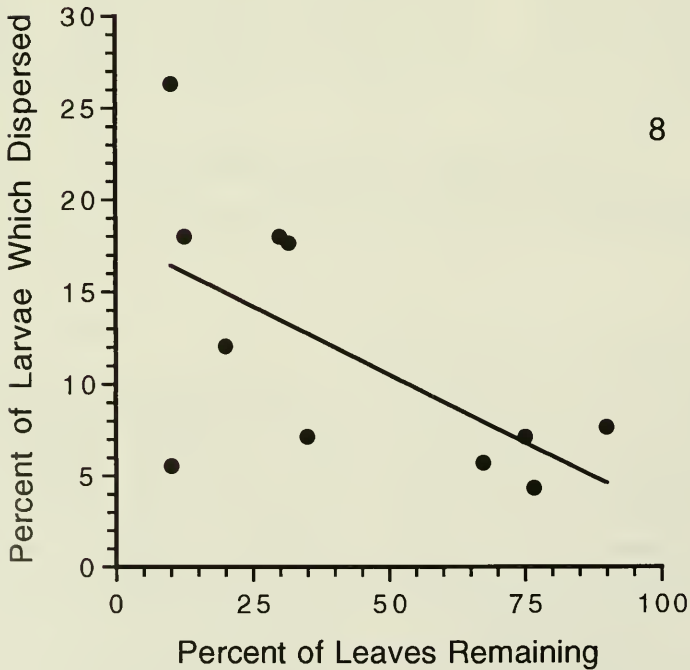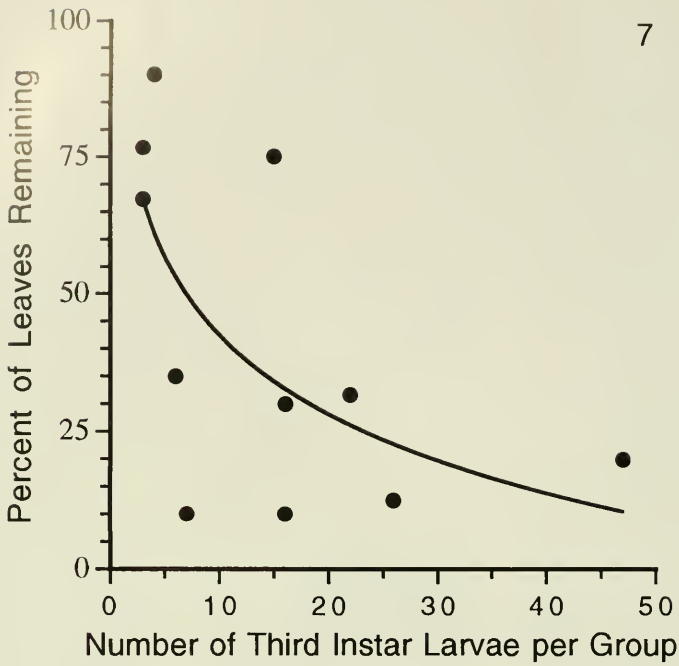
Fig. 7–8.   7, The relationship between the number of third-instar larvae per group at the onset of dispersal and the percent of leaves remaining per plant ($y = 90.1 - 47.6(x)$; $R^2 = 0.41$, $P < 0.05$). 8, The relationship between resource availability (percent of leaves remaining at the onset of dispersal) and the percent of larvae that disperse from their natal plant ($y = 17.9 - 0.15(x)$; $R^2 = 0.38$, $P < 0.05$).

ticifer system. Beginning at the third instar, the mode of feeding switches to leaf chewing, and feeding aggregations dissolve. Later-instar larvae continue to feed on the natal plant or disperse to adjacent plants. Only third-instar or later larvae are capable of dispersal, and dispersing larvae are adept at locating near-neighbor host plants. Dispersal rate from natal plants may be governed by resource availability during the third larval instar, which may be mediated by feeding group size in relation to plant size. The ecological factors underlying dispersal from natal plants deserve further attention as there seems to be a fundamental conflict between the clutch size deposited by females on plants and the amount of resources required to support development of the clutch. First- and second-instar larvae exhibit group defense, and all instars are brightly patterned with contrasting colors. The apparent lack of natural enemies, along with the gregarious nature, defensive behaviors, apparent aposematic coloration, and the chemical composition of the host plant suggest that *D. ampla* larvae are noxious to natural enemies and that the larval color pattern may function as warning coloration used to deter predation. Based on these initial observations *D. ampla* populations may be controlled by factors other than natural enemies.

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